Energy density of sub-Antarctic fishes from the Beagle Channel

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Abstract The energy density (ED) of nine species of sub-Antarctic fishes was estimated by calorimetry. The fish, seven notothenioids, one atherinopsid and one galaxiid, represents some of the more abundant species in the ichthyofauna of the Beagle Channel. Principal-components analysis (PCA) of the ED of the different organs/tissues indicated that PC_1 and PC_2 accounted for 87% of the variability. Separation along PC_1 corresponded to differences in muscle and liver energy densities whereas separation along PC_2 corresponded to differences in the ED of the gonads. Differences between species were significant except for *P. sima*. Inclusion of the gonadosomatic index (GSI) as an explanatory variable enabled us to establish the existence of energy transfer from muscle and liver to the gonads in ripe *P. tessellata* females. Total ED values varied between 4.21 and 6.26 kJ g^{-1}, the pelagic *Odontesthes* sp. being the species with the highest ED. A significant relationship between ED and muscle dry weight (DW_M) was found for all the species except *P. tessellata*. These data are the first direct estimates of ED of fishes from the Beagle Channel.

Abbreviations

EC	Total energy content
ED	Energy density
WC	Water content
WW	Wet weight
DW	Dry weight
GSI	Gonadosomatic index
HIS	Hepatosomatic index

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Introduction

There is a large literature on energy studies of aquatic organisms mostly dealing with the energy content of whole organisms, because the principal goal of those studies is the evaluation of the species as dietary items (Hecht and Cooper 1986; Paul et al. 1998; Schwarz and Hammer 1933; Smith et al. 1990). In those studies therefore, the reported values are the total body energy content, or the energy density (ED) value per gram of body (wet or dry) for each particular species in order to evaluate the different species as prey items. The quality of a prey as a source of energy is a characteristic that varies between species as a function of body composition, and the ED of each body compartment. Interspecific differences can be explained by variations in physiological features, phyletic heritage, feeding supply, or habitat. For example, pelagic schooling fish

have typically showed higher energy densities than demersal ones (Ball et al. 2007). In other types of study the energy value of the liver, the fast muscle, the ovaries, and the testis have been analyzed to gain a deeper understanding of the use of the energy in the different compartments of the organisms (Eliassen and Vahl 1982; Milton et al. 1994; Montecchia et al. 1990; Smith et al. 1990). These studies try to determine energy-storage organs or the process of energy transfer between organs. Muscle and, especially, the liver are usually proposed as energy storage organs for reproduction (Jonsson et al. 1997) or over-wintering (Morley et al. 2007).

The energy value of whole organisms, or different tissues, could be studied indirectly, by determining the proximal composition of the tissues, or directly, by burning the samples in a calorimetric bomb; both are time-consuming (Craig et al. 1978; Lucas 1996). The indirect method estimates the energy content by using the energy equivalents of carbohydrates, proteins, lipids, and ash (Brody 1945); this can introduce noise to the determinations and, therefore, the calorimetric method is more accurate. Use of empirical relationships between ED and water content (WC) to estimate energy values for new regions, new taxa, or different seasons have proved useful and more affordable (Ciancio and Pascual 2006; Ciancio et al. 2007; Hartman and Brandt 1995).

Notothenioids are a sub-order of Perciformes that are very well represented in sub-Antarctic and Antarctic waters. Seventeen species have been described in the Beagle Channel (Lloris and Rucabado 1991; López et al. 1996) including seven we are going to analyze in this study. This group comprises mainly demersal sluggish species but also includes the benthopelagic species *Eleginops maclovinus* and *Paranotothenia magellanica*. Two non-notothenioids fishes with a southern limit of distribution in the Beagle Channel were also studied—a marine pelagic atherinopsid (*Odontesthes* sp.) and the anadromous galaxiid *Galaxias maculatus*.

In this work we present ED values for each species, and ED values for different organs/tissues, of sub-Antarctic notothenioid fishes, one atherinopsid, and one galaxiid. Analysis of the different organ/tissues enabled us to evaluate interspecific differences in the use of energy in the different organs/tissues. The energy content values could be used in the construction of energy models to understand the energy structure of the marine ecosystem. We also evaluated a method for prediction of species energy densities from muscle tissue WC, which could facilitate further studies.

Materials and methods

Fish

Nine fish species were analyzed including the notothenioids *Champsocephalus esox* (Günther, 1861), *Paranotothenia magellanica* (Forster, 1801), *Patagonotothen tessellata* (Richardson, 1845), *Patagonotothen cornucola* (Richardson, 1844), *Patagonotothen sima* (Richardson, 1845), *Eleginops maclovinus* (Cuvier, 1830), and *Cottoperca gobio* (Günther, 1861); the atherinopsid *Odontesthes* sp., and the galaxiid *Galaxias maculatus* (Jenyns, 1842) (Table 1). All the notothenioids were captured using trammel nets. The silversides, *Odontesthes* sp., were captured by using gill nets. The puyen, *G. maculatus*, were captured using a small seine net. Fish were weighed (0.01 g), measured (total and standard length to the nearest millimeter), and dissected, and the gonads and liver were weighed (0.0001 g). The gonadosomatic (GSI) and the hepatosomatic (HIS) index were calculated as follows:

$$GSI = \text{gonad wet weight} * 100/\text{total weight}$$
$$HIS = \text{liver wet weight} * 100/\text{total weight}$$

Calorimetry

The different tissues/organs were dissected and weighed wet (WW). At that point some samples were frozen until processing and some were dried immediately in an oven at 60°C until constant weight (±0.0001 g) was reached, approximately 72–90 h later. This was recorded as the dry weight (DW). Previous assays have shown no differences between these two methods of processing the samples. Water content of the different tissue/organs was calculated as the difference between WW and DW and expressed as a percentage. Dry samples were ground and pelletized with a press (Parr 2812). Pellets of 100-200 mg of the different tissues/organs were burned in a micro-bomb calorimeter (1425 Parr) to obtain their caloric content, as described by Beukema and De Bruin (1979) and Lucas (1996). The caloric content of each

Table 1 Basic information about the species studied in this work

Scientific name	Common name	Family	Habit	Feeding habits	Distribution**
Paranotothenia magellanica	Maori cod	Nototheniidae*	Bentopelagic[a], Pelagic[b]	Small crustaceans, algae[a]	42°S–55°S
Patagonotothen cornucola	Rock fish	Nototheniidae*	Demersal[a]	Small crustaceans, algae[a]	41°S–54°S
Patagonotothen sima	Rock fish	Nototheniidae*	Bentopelagic[c]	Small crustaceans, algae[a]	42°S–54°S
Patagonotothen tessellata	Rock cod	Nototheniidae*	Benthic[a]	Small crustaceans, algae[a]	41°S–54°S
Champsocephalus esox	Pike icefish	Channichthyidae*	Benthopelagic[a]	Piscivorous; crustaceans[a,d]	52°S–54°S
Cottoperca gobio	Channel bullfish	Bovichthyidae*	Benthic[a]	Piscivorous, small crustaceans, algae[a]	41°S–54°S
Eleginops maclovinus	Patagonian blennie	Eleginopidae*	Benthopelagic[e]	Omnivorous and bentivorous[f]	39°S–54°S
Galaxias maculatus	Inanga	Galaxiidae	Benthopelagic[g]	Small crustaceans, terrestrial insects[h]	33°S–55°S
Odontesthes sp.	Silverside	Atherinopsidae	Pelagic[a]	Piscivorous, small crustaceans[i]	39°S–54°S

* Species that belong to suborder notothenioidei

** Northern and southern limits of the distributions

Refs.: [a] Lloris and Rucabado (1991); [b] DeWitt et al. (1990); [c] Pequeño (1989); [d] Hureau (1985); [e] Corporación de Fomento de la Producción (Chile) (1980); [f] Isla and San Román (1995); [g] Allen (1989); [h] Vila et al. (1995); [i] Lattuca (personal communication)

sample was corrected for acid content but not for ash, and was expressed as ED in kJ g^{-1} dry weight. If combustion was incomplete new pellets were made and the experiment was repeated. The calorimeter was periodically calibrated using benzoic acid as reference material.

The ED was calculated for all the notothenoids from the energy densities of muscle (ED_M), liver (ED_L), and gonads (ED_G), taking into account the WC of each organ and the proportion of each organ in relation to total weight. Muscle weight was estimated from the eviscerated weight for all the notothenioids. The method was validated by back-calculation for *Odontesthes* sp. and *G. maculatus*, species for which ED was also calculated directly by calorimetry. The back-calculated values did not differ significantly from the direct calorimetric measurements. For *Odontesthes* sp. the red muscle was included in the ED_M calculation, because it represents a significant amount of muscle weight (7.31 ± 0.41%) and because the ED of this muscle is different from that of white muscle.

Statistical analysis

Principal-components analysis (PCA) was performed with ED_M, ED_L, and ED_G as the variables, using the

software PC-ORD (McCune and Mefford 1999). The principal components were computed from the correlation matrix of the ED variables. A component can be viewed as a weighted sum where the weight of the variables on each principal component is represented by a coefficient. Statistical differences between species were analyzed using multi-response permutation procedures (MRPP).

Results

PCA using ED_M, ED_L, and ED_G as variables produced two main axes (principal components) that explained 87% of the variability of the data (Table 2). From the coefficients of the first axis it could be seen that an average of muscle and liver (coefficient of 0.7 for both variables) explained 54.2% of the variability. Thus, the specimens with higher PC_1 values were those with more ED in muscle and liver. The second axis (PC_2), which accounted for the 32.8% of the variability, was primarily related to the gonads (coefficient 0.98). The third principal component (PC_3) was neglected because it explained a relative low percentage of the total variability (Table 2). The analysis showed that

Table 2 Coefficients representing the weight of the measured variables on the three principal-components axes and the variance explained for each of them

Measured variables	Principal-components axes		
	PC$_1$	PC$_2$	PC$_3$
ED$_M$	0.69	−0.16	−0.70
ED$_G$	0.17	0.98	−0.07
ED$_L$	0.70	−0.07	0.71
Explained variance (%)	54.2	32.8	12.9

Odontesthes sp. and *P. magellanica* were clearly separated from the rest, the former species accumulating most energy in its tissues and the latter accumulating least energy (Fig. 1a). The statistical analysis showed that all the groups (species) were significantly different from the others, except *P. sima* was no different from any of the other species (Table 3). The inclusion of the GSI as an explanatory variable in the PCA analysis enabled better understanding of the energy management between muscle, liver, and gonads, at least in some species (Fig. 1b). In *P. tessellata* high GSI values corresponded to low values in axis 1, and in *Odontesthes* sp. high GSI values are independent of axis 1. When the second axis of the PCA (that mostly related with ED$_G$) was plotted against GSI values for female *P. tessellata* an increment in the value of the second axis at low GSI was evident, with the values reaching a plateau at higher GSI (Fig. 2a). No clear pattern appeared for the males. The relationship between the HSI and the GSI in female *P. tessellata* changes at a GSI value that corresponds to total maturation (Fig. 2b).

Values of ED, ED$_M$, ED$_L$, and ED$_G$ for all the studied species are presented in Table 4. The ED did not change significantly with total length, varying between 4.21 and 6.26 kJ g^{-1} dry weight. As previously reported by other researchers, we found a significant linear relationship between ED and DW (ED = −0.66 + 0.26 * DW, R^2 = 0.94, P < 0.001, Fig. 3). We also found a similar linear relationship between total ED and muscle dry weight (DW$_M$) with data from all species (ED = −0.48 + 0.26 * DW$_M$, R^2 = 0.87, P < 0.001, Fig. 4a). The only species with a significant number of individuals for which regression deviates significantly for the model was *P. tessellata* (ED = 0.35 + 0.22 * DW$_M$, R^2 = 0.74, P < 0.001, Fig. 4b).
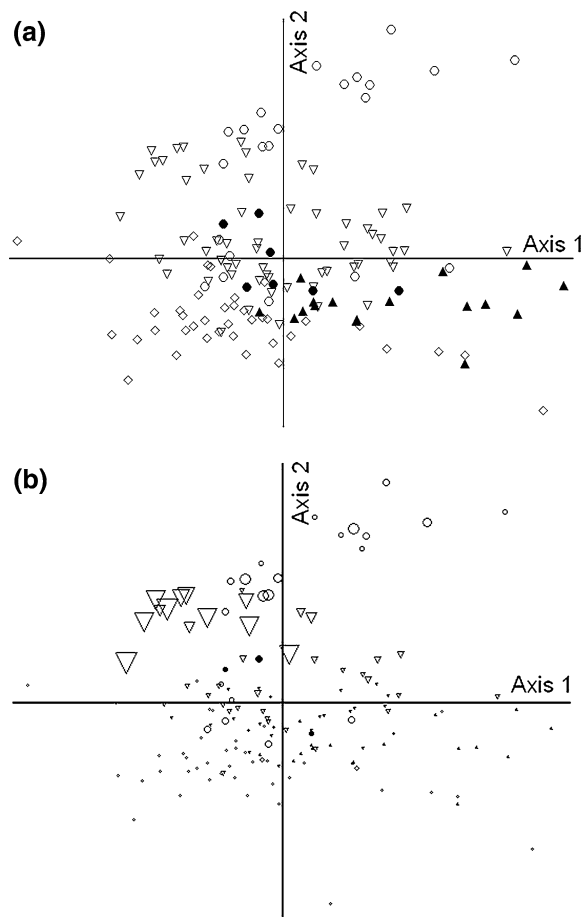

Fig. 1 PCA analysis showing the main two axis that explain together 87% of the variation for the five most abundant species in this study. (**a**) The species *Odontesthes* sp. and *P. magellanica* showed the highest and lowest energy densities, respectively. (**b**) By making symbol sizes proportional to GSI values it could be seen that all the mature *P. tessellata* where located at low values of the first axis (liver and muscle). This suggests transfer of energy from the muscle and liver to the gonads. Symbols: *empty diamonds*, *P. magellanica* (n = 39); *filled circles*, *P. sima* (n = 7); *empty circles*, *Odontesthes* spp. (n = 22); *filled triangles*, *E. maclovinus* (n = 17); *inverted empty triangles*, *P. tessellata* (n = 59)

Discussion

PCA analysis, with a first axis (a combination of muscle and liver) explaining more than 50% of the total variation of the data and a second axis (mainly influenced by the gonads) explaining 32% of the total variation, enabled us to separate significantly all the species but *P. sima* (Table 3 and Fig. 1a). *Odontesthes* sp. was undoubtedly the species with highest energy content (note the specimens with high values

Table 3 MRPP pairwise comparisons

Species comparison	P-value
P. magellanica vs. *Odontesthes* sp.	0.0000*
P. magellanica vs. *E. maclovinus*	0.0000*
P. magellanica vs. *P. tessellata*	0.0000*
P. magellanica vs. *P. sima*	0.0059
P. sima vs. *Odontesthes* sp.	0.0059
P. sima vs. *E. maclovinus*	0.0071
P. sima vs. *P. tessellata*	0.347
Odontesthes sp. vs. *E. maclovinus*	0.0000*
Odontesthes sp. vs. *P. tessellata*	0.0000*
E. maclovinus vs. *P. tessellata*	0.0000*

Post-hoc comparisons or contrast between groups. P critical used was corrected by multiple comparisons, P critical = 0.005. * Significant differences

for both axes in Fig. 1a). This was expected from our histological data for this species, which has large amounts of lipids in its red muscle (Calvo et al., unpublished results). This characteristic also fits with the hypothesis of pelagic species being those with the highest energy contents (Ball et al. 2007). Among the notothenioids habitat did not explain differences in energy content, because *P. magellanica*, the most pelagic species (Vanella et al. 2007), was the one with the lowest energy content. *P. magellanica* is, however, a species that relies on continuous swimming to keep a position in the water column (Fernandez et al., unpublished results) and should, therefore, expend energy on that activity. Moreover, sexually ripe individuals were never captured in the field and we could, therefore, be underestimating the energy content of the species as a whole when comparing with other species that include ripe individuals, for example *P. tessellata*.

When GSI values of the different individuals were included as explanatory variables in PCA we found that all the mature *P. tessellata* where located at low values of the first axis (liver and muscle), suggesting transfer of energy from the muscle and liver to the gonads (note the size of the symbols in Fig. 1b). This kind of energy transference from muscle and liver to the gonads has previously been reported for other species of notothenioids (Kamler 2001; Vanella et al. 2005) and non-notothenioids (Fiorin et al. 2007; Zaboukas et al. 2006). Analysis of the ED_G in *P. tessellata* separated by the sex of the individuals showed a clear influence of a well known physiological
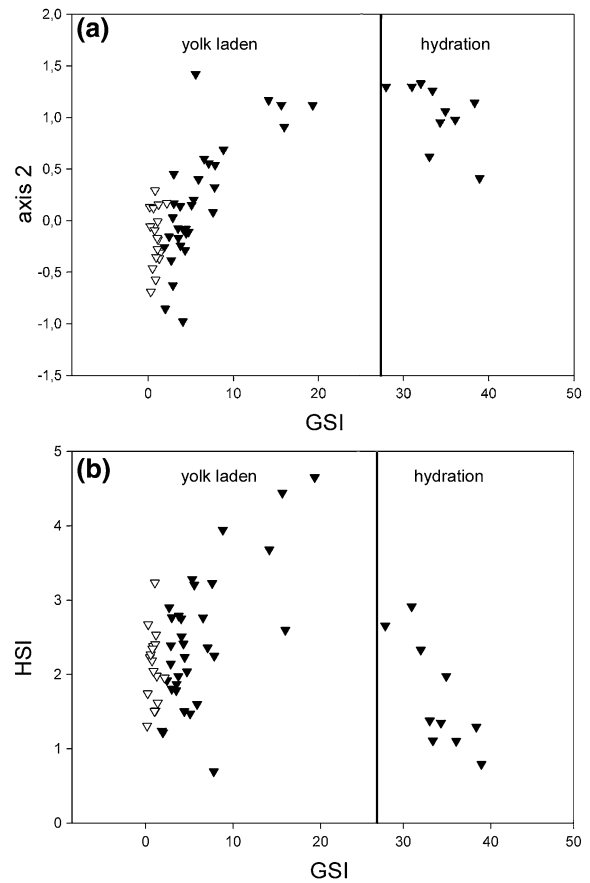

Fig. 2 Variation of the GSI during the oocytes' yolk-laden and hydration periods. (**a**) Second axis of the PCA versus gonadosomatic index (%) for *P. tessellata* ($n = 59$). Females showed a clear separation of the oocyte yolk-laden and the oocyte hydration periods. (**b**) Hepatosomatic index (%) versus gonadosomatic index (%) for *P. tessellata* ($n = 59$). Symbols: *empty triangles*, males; *filled triangles*, females

mechanism (Fig. 2a). Previous studies on reproduction of *P. tessellata* in our laboratory indicated that in ovaries with yolk-laden oocytes GSI values ranged between 8.18 and 28.68, with a mean of 13.39, whereas in ripe ovaries, when oocytary hydration occurs, the GSI values ranged between 28.02 and 42.63 (Rae 1991; Rae and Calvo 1995). The ED_G in *P. tessellata* females varied in accordance with the process of yolk accumulation. The ED of the ovary increased during yolk deposition and when the GSI reached the value of 28 the ED remained constant, because the oocytes no longer incorporate extra matter other than water. The increase in the HSI and the GSI values during the oocyte yolk-laden period (Fig. 2b, GSI < 28) would correspond to vitellogenin synthesis in the liver and its

Table 4 Energy densities and water content of the studied species

| Scientific name	Energy density (kJ g⁻¹ dry weight)					Water content (%)					Energy density (kJ g⁻¹ Wet weight)
	Muscle	Liver	Testes	Ovaries	Total	Muscle	Liver	Testes	Ovaries	Total	Total
P. magellanica	22.40 ± 1.21	25.12 ± 2.44	20.80 ± 1.53	20.88 ± 0.65	22.59 ± 1.03	78.79 ± 4.24	73.29 ± 5.90	84.06 ± 4.52	82.74 ± 3.18	78.96 ± 2.75	4.75 ± 0.71
P. cornucola	21.72	23.53	–	23.02 ± 1.05	22.06	78.49 ± 2.40	72.54	–	73.55 ± 8.31	75.75	5.35
P. sima	23.03 ± 0.98	25.13 ± 1.57	22.11 ± 0.34	22.57 ± 0.77	23.08 ± 095	78.42 ± 1.03	74.11 ± 4.67	89.34 ± 2.96	76.14 ± 4.14	78.45 ± 1.14	4.98 ± 0.36
P. tessellata	22.40 ± 0.74	26.07 ± 2.87	22.11 ± 0.51	22.84 ± 1.11	22.64 ± 0.67	78.43 ± 2.73	70.97 ± 6.15	83.77 ± 3.12	75.74 ± 8.07	77.68 ± 3.04	5.06 ± 0.72
C. esox	23.12 ± 0.27	26.89 ± 0.34	–	23.40 ± 0.42	23.18 ± 0.28	81.39 ± 2.28	71.45 ± 1.16	–	80.71 ± 0.55	80.36 ± 0.39	4.55 ± 0.04
C. gobio	21.81 ± 0.01	23.64 ± 2.21	23.69 ± 1.86	–	21.82	77.42 ± 4.17	68.96 ± 7.75	86.16	–	80.70	4.21
E. maclovinus	23.95 ± 1.10	28.63 ± 2.18	21.8 ± 0.55	21.70 ± 0.61	23.99 ± 1.10	76.06 ± 3.87	67.81 ± 5.59	81.52 ± 1.71	81.59 ± 1.53	75.63 ± 2.20	5.86 ± 0.71
G. maculatus	–	–	–	–	24.89 ± 0.96	–	–	–	–	79.95 ± 1.35	5.01 ± 0.30
Odontesthes sp.	23.83 ± 1.25	26.51 ± 3.20	21.96 ± 0.41	25.74 ± 1.03	23.74 ± 0.58	73.97 ± 2.67	61.98 ± 9.45	78.39 ± 3.12	67.99 ± 6.72	73.65 ± 3.00	6.26 ± 0.78
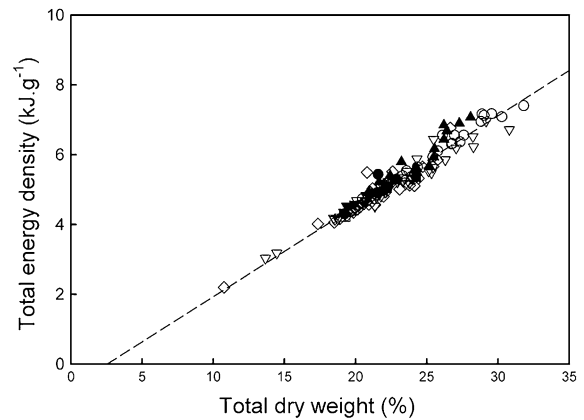
Fig. 3 Relationship between total energy density (ED, kJ g⁻¹ wet weight) and total dry weight (DW, %) given by the equation: ED = −0.66 + 0.26 DW, R^2 = 0.94. Symbols: *inverted filled triangles*, *C. esox* (*n* = 2); *empty squares*, *C. gobio* (*n* = 1); *empty diamonds*, *P. magellanica* (*n* = 39); *filled squares*, *P. cornucola* (*n* = 1); *filled circles*, *P. sima* (*n* = 7); *empty circles*, *Odontesthes* spp. (*n* = 32); *filled triangles*, *E. maclovinus* (*n* = 17); *inverted empty triangles*, *P. tessellata* (*n* = 58)

transfer to the ovary, something that has also been suggested for other fishes (Galloway and Munkittrick 2006). The continuous increase of GSI values (Fig. 2b, GSI > 28) is because of oocyte hydration, and the fall in the HSI values would correspond to the arrest in the production of vitellogenin in the liver.

Use of energy models in ecology has grown increasingly since the early fifties. Energy values to fit those models have varied from ED (expressed per wet or dry weight) to energy content. Previous studies have found a robust relationship between ED and total dry weight of fish (Ciancio et al. 2007; Hartman and Brandt 1995). These models enabled simplification of the technique, substituting time-consuming calorimetry or proximal analysis for the easier calculation of WC for the whole specimen, which is faster and requires no specialized equipment other than an oven. In order to create a useful tool for further studies in the Beagle Channel we investigated the relationship between total energy content, ED, and total and muscle WC of common species of the area. We hypothesized that we could go further and estimate ED of the whole specimen from WC of one tissue, the muscle. The data from all the species showed a strong relationship between total ED and muscle dry weight, enabling the use of the latter as a predictor of total ED for all species except *P. tessellata*, which deviates significantly from the model.
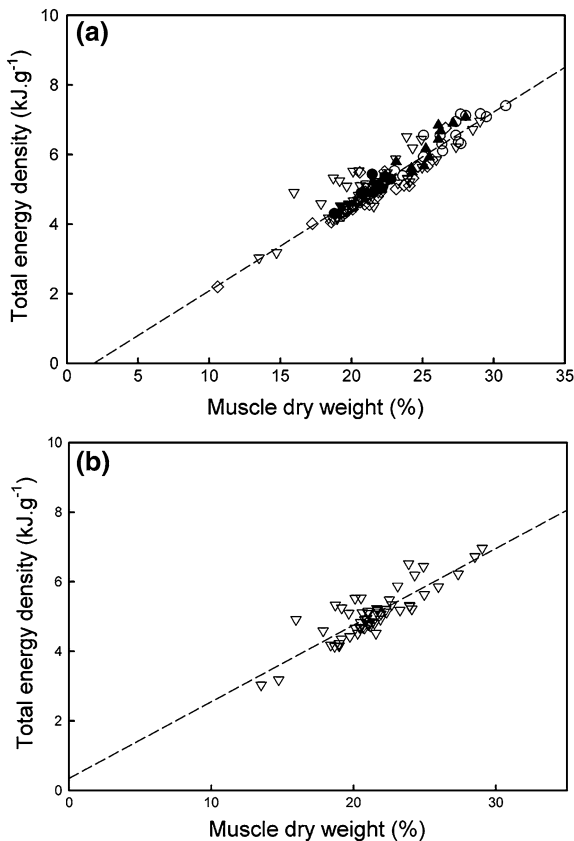
Fig. 4 Relationship between total energy density (ED, kJ g^{-1} wet weight) and muscle dry weight (DW$_M$, in percentage). (**a**) all the species analyzed in this study except *G. maculatus*. Relationship given by the equation: ED = $-0.48 + 0.26$ DW$_M$, $R^2 = 0.87$. Symbols: *inverted filled triangles*, *C. esox* (*n* = 4); *empty squares*, *C. gobio* (*n* = 9); *empty diamonds*, *P. magellanica* (*n* = 83); *filled squares*, *P. cornucola* (*n* = 3); *filled circles*, *P. sima* (*n* = 22); *empty circles*, *Odontesthes* spp. (*n* = 22); *filled triangles*, *E. maclovinus* (*n* = 62); *inverted empty triangles*, *P. tessellata* (*n* = 101). (**b**) *P. tessellata*. Relationship given by the equation: ED = 0.35 + 0.22 DW$_M$, $R^2 = 0.74$

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